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Variation in Production and Seasonal Development of Mountain Grasslands in Western Montana

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RESEARCH SUMMARY

A 10-year study of mountain grasslands indicated that although total herbage production can differ as much as 200 percent between good and poor years, in 2 out of 3 years it can be expected to be within 85 to 90 percent of the long-term mean; production of forbs can vary as much as 250 percent between years, yet two-thirds of the time be within 80 to 85 percent of the long-term mean; total production of graminoids may differ as much as 275 percent between years, yet remain within 75 percent of their mean two-thirds of the time. Yearly variability in production of individual species is usually much greater. Weather-based models accounting for this production variability differ appreciably between nearby sites on different exposures. Although the greatest yearly difference in the beginning of growth in the spring for most species was from 25 to 30 days, in 2 out of 3 years the beginning of growth can be expected to be within 8 to 12 days of long-term means. The date of flowering of early-blooming species is twice as variable as that of late-blooming species. Yearly variation in start of seed dissemination was highly species dependent; the maximum difference between years ranged from 3 to 6 weeks. Two-thirds of the time seed dissemination can be expected to begin within 6 to 8 days and plant drying within 12 days of long-term means. Although growth and flowering began about 1 week later on northeast than on southwest exposures, no consistent difference existed between exposures in date of seed dissemination or in growth duration. Early growth appeared most closely associated with May and June temperatures. Vegetation readiness for grazing can differ as much as 5 weeks over a 10-year period, but can be expected to be within 2 weeks of the long-term mean in 2 out of 3 years.

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INTRODUCTION

The rate of plant development and the total amount of growth produced on native rangelands can vary greatly from year to year. These variations in development and yield are vital considerations in planning proper grazing management. In addition, knowledge of the growth of individual plant species as affected by yearly variations in weather is fundamental to understanding the dynamics of grassland ecosystems.

Despite the conspicuousness and importance of plant growth variations attributable to weather, these variations have been documented for few of the major range types in the West. Numerous workers have related total forage production to specific weather variables (Smoliak 1956; Johnston and others 1969; McLean and Smith 1973; Shiflet and Dietz 1974; Sneva 1977; Wight and Hanks 1981), but relatively few have attempted to describe the overall dynamics of range plant communities in relation to weather. Blaisdell's (1958) study of the sagebrush-grass range in southeastern Idaho is a notable example of such a comprehensive description of growth variations in plant communities.

Mountain grasslands are highly valued summer range for domestic livestock as well as for big-game animals in the mountainous West; this is particularly true in the Northern Rocky Mountains. To document the annual variation in plant development and herbage yield on a portion of this major range type, I conducted a study on both northerly and southerly exposures at two elevations on the Gravelly Range in southwestern Montana. Earlier I published the variations that occurred in plant growth over the initial 5-year period of this study and discussed the differences between elevations and exposures (Mueggler 1972a). A companion publication (Mueggler 1971) treats in detail variations in weather factors measured at the same locations and time. The study was continued for an additional 5 years on two exposures, but just at one elevation, to build a better data base for relating variations in weather to plant growth. The results of this 10-year study are reported here.

STUDY AREA

The two long-term study sites were near the north end of the Gravelly Range, approximately 12 miles (20 km) southwest of Virginia City in southwestern Montana. The sites were located on typical southwestern Montana mountain grasslands at 7,100 ft (2 164 m) elevation on opposing slopes approximately 590 ft (180 m) apart. One site was on a southwest exposure with 7-percent slope; the other was on a northeast exposure with 12-percent slope. Annual precipitation averaged approximately 20 inches (50 cm).

Soils of the area were derived from highly weathered residual limestone. The soil on the southwest exposure was a clayey-skeletal Calcic Cryoboroll with a 17-inch (43-cm) deep solum containing abundant rock fragments. That on the northeast exposure was a fine Calcic Cryoboroll with a 20-inch (51-cm) deep solum relatively free of rock. Both had ustic moisture and cryic temperature soil climatic regimens.

Vegetation of the general area (fig. 1) was a mosaic of mountain grasslands and coniferous forests comprised primarily of limber pine (*Pinus flexilis*), lodgepole pine (*Pinus contorta*), and Douglas-fir (*Pseudotsuga menziesii*). Vegetation on the grassland study sites consisted of variations in the Idaho fescue (*Festuca idahoensis*)/bluebunch wheatgrass (*Agropyron spicatum*) habitat type (Mueggler and Stewart 1980). The southwest sloping site was typical of this type, whereas the northeast sloping site represented the western needlegrass (*Stipa occidentalis*) phase of the habitat type with more moisture available for plant growth. The Idaho fescue/bluebunch wheatgrass habitat type is considered to be one of the most abundant mountain grassland types in southwestern Montana (Mueggler and Stewart 1980).

METHODS

Herbage production was determined from 1964 through 1973 by sampling 50 permanent 4.8 ft^2 (0.45 m^2) plots on each study site. These plots were distributed in a series of 10 sets, 5 plots per set, over a relatively

Figure 1.—Mountainous rangelands in southwestern Montana, typical of the vegetation and terrain of the study sites, often consist of a mosaic of tussock grasslands and coniferous forests.

uniform portion of the site. Peak standing crop of the current year's biomass was measured when the vegetation appeared to have achieved full growth and just before many species began to dry. This generally occurred between the middle and end of July.

Production was determined by combining percent-weight estimates and clipping, because estimating species weights as a percentage of total yield is believed to be more efficient than estimating directly as weight units (Hutchings and Schmautz 1969). Each year one plot in each set of five was protected from livestock grazing by a wire cage. This plot was considered the reference plot for that set for that particular year. The reference plot was changed each year so that no one plot served as a reference more than once in 5 years. Total herbage production on each of the remaining four plots in a set was estimated as a percentage of the total production on the set's reference plot. These estimates were adjusted to compensate for current livestock utilization, which usually was slight. The weight of each species on a plot was then estimated as a percentage of the total production on the plot; these estimates were also adjusted to compensate for utilization. Total vegetation on the reference plot was then clipped to ground level and weighed, with individual weights of the four major species on the plot recorded separately. Comparing the estimated percent-weight on the reference plot with the computed percent-weight for each of the clipped species served as a continual check on the accuracy of the estimates and permitted the estimator to adjust for drift in his estimates. The total production on the clipped reference plot was used to translate the percentage figure for total production on the estimated plots to actual weight. The green weight of individual species on each plot could then be computed from their respective percentages. The clipped material was subsequently dried, the percentage dry matter obtained for all important species, and all green weights converted to production of air-dry material.

I originally thought that clipping one-fifth of the plots to ground level every year would not affect overall production estimates appreciably in subsequent years. It became apparent, however, that the initial decline in vegetation vigor on the clipped plots persisted longer than anticipated. I therefore established a new series of 50 plots parallel to the existing plots on each site. Both old and new plots were inventoried in the same year to provide for the minor adjustment factors needed to

equate the new plots with the old. Production for 1970 through 1973 is from the adjusted second series of plots.

Developmental growth stage was recorded for common species at each site at weekly intervals. Individual plants of selected species were marked for repeated observation; 40- by 80-ft (12- by 24-m) enclosures protected these plants from livestock. Dates of various development stages for each species were determined from the marked plants plus supplemental observations of the development of surrounding plants. If development of a marked individual appeared abnormal, a more typical specimen was selected for subsequent observation. The sites were visited each week from the onset of active growth in the spring (usually early May) until most species were dormant (late October).

The developmental stages discussed in this report are:

Forbs

Growth starts—first evidence of current year's growth.

First bloom—first fully developed blossoms.

Bloom over—approximately 90 percent of flowering completed.

Dissemination starts—first evidence of seed drop.

Plant dried—at least 90 percent of the herbage dried.

Grasses

Growth starts—first evidence of current year's growth.

Flower stalks appear—first evidence of booted flowering culms.

Flowers in bloom—approximately 25 percent of flowers in anthesis.

Seed ripe—approximately 25 percent of seed mature as judged by hardness of the caryopsis.

Plant dried—at least 90 percent of the herbage dried.

Weather was monitored on each site from May 1 to October 31 each year. Usually the snowpack had melted on the southwest exposure by late April and on the northeast exposure about 1-1/2 weeks later in early May. Although occasional snowstorms were not unusual in May, June, September, and October, the winter snowpack generally did not begin to accumulate until sometime in November. Instruments were placed on each site to measure air and soil temperature, relative humidity, precipitation, soil moisture, wind, and solar radiation. These instruments were within a 40- by 80-ft (12- by 24-m) enclosure at least 10 ft (3 m) from the barbed-wire fence.

Air temperature and relative humidity were recorded continuously by a hygrothermograph installed 4.5 ft (1.4 m) above ground in a standard shelter. Soil surface temperatures were continuously recorded in the sun and in the shade by a soil thermograph; a continuous record of temperature was also obtained at a 2-inch (5-cm) depth. Duplicate readings of soil temperature and soil moisture at 8, 20, and 40 inches (20, 50, and 100 cm) were taken at weekly intervals by use of Colman fiberglass soil moisture units buried in undisturbed soil beneath existing vegetation. Recording precipitation gages shielded by wind deflectors measured periodicity, intensity, duration, and total fall. The amount of wind each site received was measured by totalizing 3-cup anemometers mounted 6 ft (1.8 m) above ground and read weekly. Solar radiation was continuously recorded by bimetalic actinographs.

A total of 90 weather variables were compiled for possible correlation with plant growth. Of these, 20 were subjectively chosen as most likely to have a bearing upon herbage production and 7 selected as likely to affect plant development. The relationships between weather and plant growth discussed in this report are based upon correlation and regression analyses with these selected weather variables. Only the vegetation classes and more productive species were evaluated.

RESULTS AND DISCUSSION

Production Variability

Production of vegetation on the northeast exposure was almost double that on the southwest exposure. In 9 of the 10 years it ranged from 172 to 235 percent of that on the southwest exposure. This production difference was comprised principally of forbs. Very likely this difference can be attributed to a greater availability of soil moisture for growth on the northeast exposure, stemming from less evaporative loss, greater storage capacity in the soil mantle, and differences in snow accumulation because of blowing and drifting patterns.

Total vegetation production varied appreciably between years (table 1). Production during the best year on the southwest exposure was approximately 1-1/3 that during the poorest year, whereas the best year on the northeast exposure was over twice that of the poorest year. The coefficient of variation for total production over the 10-year period was 12 percent on the southwest exposure and 19 percent on the northeast exposure. During the first year of the study, however, total production on the northeast exposure was inexplicably low (724 lb/acre [811 kg/ha] compared to 1,217 lb/acre [1 364 kg/ha] for the next lowest year) and unalined with production on the southwest exposure. Discarding this one value resulted in a mean production of 1,377 lb/acre (1 544 kg/ha) with a coefficient of variation of 10 percent on the northeast site. In this case the relative variability in total production between years would be approximately the same on both sites irrespective of the productivity levels of the sites. This agrees with the conclusions of Mueggler and Stewart (1981) that there is no pronounced difference between good and poor sites in the proportionate amount of variability between years in total standing crop.

The amount of yearly variability in production by vegetation classes considerably exceeded that of total production. The southwest exposure produced well over two-times as much graminoids and 1-1/2 times as much forbs in the highest year than in the lowest year; the northeast exposure varied more yet in that it produced 2-3/4 times as much graminoids and 2-1/2 times as much forbs in the high than in the low year (table 1). The coefficient of variation between years for graminoids on both sites approached 25 percent; it was 14 percent for forbs on the southwest sloping site and 21 percent on the northeast sloping site. Interestingly, annual production of graminoids was not related to the annual production of forbs. The nonsignificant correlation coefficients

Table 1a.—*Range, mean, and standard deviation (s) of herbage production over a 10-year period*

Species	Southwest exposure Range	Southwest exposure Mean	Southwest exposure s	Northeast exposure Range	Northeast exposure Mean	Northeast exposure s
	kg/ha, air dry					
Total vegetation	663-917	767	94	811-1793	1471	272
Total graminoids	270-586	407	101	228- 628	446	114
Total forbs	276-422	359	51	583-1451	1024	216
GRAMINOIDS						
Agropyron spicatum	25-142	65	38	16- 111	43	28
Agropyron caninum	-	-	-	< 1- 11	4	3
Bromus anomalous	-	-	-	6- 17	10	4
Carex filifolia	30- 57	42	9	1- 14	7	5
Carex stenophylla	12- 45	22	11	-	-	-
Danthonia intermedia	-	-	-	24- 233	115	78
Festuca idahoensis	163-374	248	71	82- 246	170	41
Koeleria cristata	9- 18	15	3	< 1- 15	4	4
Poa spp.	< 1- 15	4	5	< 1- 15	4	5
Stipa occidentalis	7- 29	13	8	25- 100	63	25
FORBS						
Achillea millefolium	10- 50	26	13	13- 67	40	16
Agoseris glauca	19- 43	29	7	1- 66	20	20
Anemone patens	2- 7	4	2	7- 61	36	16
Antennaria rosea	10- 35	21	7	3- 21	10	4
Arenaria congesta	< 1- 20	10	6	25- 78	42	16
Astragalus miser	< 1- 9	3	3	< 1- 12	5	4
Besseya wyomingensis	< 1- 3	< 1	< 1	-	-	-
Campanula rotundifolia	9- 16	14	4	5- 35	19	10
Cerastium arvense	17- 42	26	8	26- 155	72	36
Clematis hirsutissima	-	-	-	5- 32	19	9
Erigeron subtrinervis	-	-	-	42- 130	87	24
Eriogonum umbellatum	-	-	-	34- 100	59	19
Frasera speciosa	14- 39	23	9	-	-	-
Gaillardia aristata	14- 34	23	6	13- 76	26	18
Galium boreale	30- 72	49	13	19- 55	28	10
Gentiana affinis	2- 13	5	3	-	-	-
Geranium viscosissimum	-	-	-	71- 186	114	40
Geum triflorum	2- 14	7	4	51- 156	109	29
Gilia congesta	< 1- 7	2	2	-	-	-
Linum perenne	2- 30	13	11	< 1- 9	3	4
Lupinus serecius	-	-	-	110- 263	167	55
Myositis sylvatica	-	-	-	< 1- 23	9	8
Oxytropis serecia	1- 6	4	1	-	-	-
Pedicularis contorta	38- 67	48	10	-	-	-
Phlox hoodii	1- 5	3	1	-	-	-
Phlox multiflora	-	-	-	27- 118	67	35
Polygonum bistortoides	-	-	-	< 1- 7	3	2
Potentilla gracilis	-	-	-	< 1- 22	5	6
Taraxicum officinale	< 1- 4	2	2	-	-	-
Townsendia mensana	< 1- 3	1	1	-	-	-
Viola adunca	-	-	-	46- 126	94	25
Zygadenus venenosus	< 1- 6	2	2	< 1- 11	3	3

Table 1b.—*Range, mean, and standard deviation (s) of herbage production over a 10-year period*

Species	Southwest exposure			Northeast exposure		
	Range	Mean	s	Range	Mean	s
	lb/acre, air dry					
Total vegetation	592–818	684	84	724–1599	1312	243
Total graminoids	241–523	363	90	203– 560	398	102
Total forbs	246–376	320	46	520–1295	914	193
GRAMINOIDS						
Agropyron spicatum	22–127	58	34	14– 99	38	25
Agropyron caninum	–	–	–	< 1– 10	3	3
Bromus anomalous	–	–	–	5– 15	9	3
Carex filifolia	27– 51	38	8	1– 12	7	4
Carex stenophylla	10– 40	20	10	–	–	–
Danthonia intermedia	–	–	–	21– 208	103	69
Festuca idahoensis	146–333	222	64	73– 220	152	37
Koeleria cristata	8– 16	13	3	< 1– 13	4	4
Poa spp.	< 1– 14	4	5	< 1– 13	4	4
Stipa occidentalis	6– 26	12	7	22– 89	56	22
FORBS						
Achillea millefolium	9– 45	23	12	12– 60	34	14
Agoseris glauca	17– 38	26	6	1– 59	18	18
Anemone patens	2– 7	4	2	6– 55	32	15
Antennaria rosea	9– 31	18	7	3– 19	9	4
Arenaria congesta	< 1– 18	9	6	22– 70	38	14
Astragalus miser	< 1– 8	3	2	< 1– 11	4	4
Besseya wyomingensis	< 1– 2	< 1	< 1	–	–	–
Campanula rotundifolia	8– 14	12	3	4– 31	17	9
Cerastium arvense	15– 38	23	8	23– 138	64	32
Clematis hirsutissima	–	–	–	4– 28	17	8
Erigeron subtrinervis	–	–	–	39– 116	78	23
Eriogonum umbellatum	–	–	–	30– 89	44	17
Frasera speciosa	13– 34	21	8	–	–	–
Gaillardia aristata	12– 30	21	6	12– 68	23	16
Galium boreale	26– 64	44	11	17– 49	25	9
Gentiana affinis	2– 11	5	3	–	–	–
Geranium viscosissimum	–	–	–	64– 166	102	35
Geum triflorum	2– 13	7	3	45– 139	98	26
Gilia congesta	< 1– 6	2	2	–	–	–
Linum perenne	2– 27	12	10	< 1– 8	3	3
Lupinus serecius	–	–	–	98– 235	149	49
Myositis sylvatica	–	–	–	< 1– 21	8	7
Oxytropis serecia	1– 6	3	2	–	–	–
Pedicularis contorta	34– 59	43	9	–	–	–
Phlox hoodii	1– 5	3	1	–	–	–
Phlox multiflora	–	–	–	24– 105	60	31
Polygonum bistortoides	–	–	–	< 1– 6	2	2
Potentilla gracilis	–	–	–	< 1– 20	5	6
Taraxicum officinale	< 1– 4	2	2	–	–	–
Townsendia mensana	< 1– 3	1	1	–	–	–
Viola adunca	–	–	–	41– 112	84	23
Zygadenus venenosus	< 1– 5	2	2	< 1– 10	2	3

(r) between these two vegetation classes were −0.42 on the southwest site and 0.29 on the northeast site. Apparently, the interactions of the many factors constituting "weather" on these mountain grasslands differentially affected the grasses and forbs. These findings contrast somewhat with those of Blaisdell (1958) who, over a 13-year period on sagebrush-grass range, obtained a coefficient of variation of 29 percent for graminoids and 23 percent for forbs, and a significant positive correlation in production between the two (r = 0.64*).[1]

Although forb production on the southwest exposure over the 10-year period was significantly correlated with forbs on the northeast exposure (r=0.64*), the production of graminoids was not correlated between exposures.

The relative variation in production between years was frequently greater yet for individual species (table 1). The very great difference between years in relative amounts of some minor species that contribute little to overall production was probably caused by sampling inadequacies. Some major species such as *Agropyron spicatum*, *Danthonia intermedia*, and *Stipa occidentalis*, however, produced between four and nine times more during the best than during the poorest year. These species had coefficients of variation ranging from 40 to 67 percent. The production of other major species did not fluctuate so greatly. *Festuca idahoensis*, *Erigeron subtrinervis*, *Lupinus serecius*, and *Geranium viscosissimum* varied less than 300 percent among years, and had coefficients of variation between 24 and 35 percent. Correlation in yearly production between major graminoid species was poor, with two exceptions: *Agropyron spicatum* was significantly positively correlated with *Festuca idahoensis* (r = 0.76**) on the southwest exposure, and negatively correlated with *Danthonia intermedia* (r = −0.64*) on the northeast exposure. Yearly production of only three major forbs was significantly correlated; these were *Geranium viscosissimum* and *Erigeron subtrinervis* (r = 0.87**), *Geranium viscosissimun* and *Lupinus serecius* (r = 0.71*), and therefore *Erigeron subtrinervis* and *Lupinus serecius* (r = 0.66*). These findings support Blaisdell's (1958) conclusions that (a) individual species vary greatly in their response to the same environmental factors, and (b) increased yield of one can compensate for decreased yield of another and thus dampen oscillations in total production.

Relationship of Production to Weather

The 20 weather variables selected as most likely affecting plant yield are shown in tables 2 and 3, as are their respective correlation coefficients with major plant species and vegetation classes on both sites. Surprisingly few of these individual weather variables were significantly correlated with the production of major species or of vegetation classes. More disturbing, some of the highest correlations appear at first glance to be contrary to ecological expectation. More significant correlations appeared on the less productive southwest sloping site than on the northeast site.

Agropyron spicatum production on both sites and *Festuca idahoensis* and *Galium boreale* production on the southwest exposure were slightly favored by cool June air temperatures, while the production of *Danthonia intermedia* and *Achillea millefolium* was favored by warm June temperatures. Cool July soil temperatures appeared to favor somewhat the production of *Carex filifolia*, *Carex stenophylla*, and *Achillea millefolium*. Windy May weather stimulated *Festuca idahoensis* and *Galium boreale* on the southwest exposure and *Agropyron spicatum* on the northeast exposure, but inhibited *Carex filifolia* and *Achillea millefolium*. May, June, and July precipitation appeared to favor production of *Geum triflorum*, perhaps by extending its growing period, whereas May precipitation favored *Stipa occidentalis*, and precipitation the prior fall favored *Danthonia intermedia*. Strong negative correlations were found between the production of *Agropyron spicatum* and precipitation the prior fall on both the southwest (r = −0.91**) and northeast (r = −0.89**) exposures; similiar negative correlations were found for *Festuca idahoensis* (r = −0.86**) and *Pedecularis contorta* (r = −0.74**) on the southwest exposure. These negative correlations generally carried through to the amount of soil moisture at the beginning of plant growth in the spring, which is sensible since fall precipitation and soil moisture in the spring are closely related.

This strong negative effect of fall precipitation on the following year's production of major mountain grassland species is surprising in light of the positive correlations previously reported for various range types. For example, Johnston and others (1969) found positive correlations (r = 0.75** to 0.82**) between fall soil moisture and the following year's yield of *Festuca scabrella* rangelands in southern Canada, and Sneva (1977) found that yields of *Agropyron desertorum* in southeastern Oregon were positively correlated (r = 0.75**) with July through May precipitation.

A likely explanation for my negative correlations lies in a probable negative relationship on these mountain grasslands between fall regrowth and production the following year. Active summer growth of *Agropyron spicatum* and *Festuca idahoensis* on these sites generally ceases and plants begin to cure in early to mid-August because of inadequate soil moisture to support growth (Mueggler 1971, 1972a). Appreciable late summer and early fall precipitation frequently results in fall regrowth, particularly of bunchgrass, but other plants as well if air and soil temperatures are amenable for growth. McIlvanie (1942) found the depletion of carbohydrate reserves by the initial phases of fall regrowth in *Agropyron spicatum* to parallel that ordinarily occurring during initial spring growth. Trlica and Cook (1972) observed that fall regrowth caused reductions in total available carbohydrate reserves in *Agropyron cristatum* and *Elymus junceus*, and that increasing the amount of fall regrowth by watering caused significant reductions of available carbohydrate levels which were not replenished before fall quiescence. The positive effect of levels of stored reserves on subsequent production was

[1] * indicates significance at the 95-percent probability level, and ** at the 99-percent level.

Table 2.—*Correlation coefficients (r) between selected weather factors and dry herbage production by vegetation classes and major species on a shallow soil, southwest exposure, 7,100 ft (2 164 m) elevation site (probability: * = >95%; ** =>99%)*

Weather factors	Total vegetation	Total graminoids	Total forbs	*Agropyron spicatum*	*Festuca idahoensis*	*Carex filifolia*	*Carex stenophylla*	*Achillea millefolium*	*Agoseris glauca*	*Galium boreale*	*Pedicularis contorta*
Precipitation											
Prior Sept. thru Oct.	-0.83*	-0.93**	0.36	-0.91**	-0.86**	0.39	0.50	0.58	0.29	-0.48	-0.74*
May	.22	.12	.14	.17	.01	-.12	-.11	.13	-.01	-.51	.48
June	.50	.50	-.06	.39	.33	.41	-.01	-.28	-.03	.26	.28
July	.07	-.12	.35	01	-.20	.14	.01	.16	.06	-.16	-.01
May + June	.61	.54	.03	.48	.32	.32	-.07	-.19	-.03	-.06	.55
May + June + July	.53	.39	.19	.40	.17	.33	-.05	-.08	.01	-.12	.45
Prior Sept.-Oct., + May-July	-.01	-.24	.47	-.22	-.44	.65*	.31	.33	.21	-.48	-.04
Soil moisture at 100 cm[1]											
At beginning of growth	.40	.69*	-.64*	.74*	.72*	-.55	-.77**	-.85**	-.60	-.61	.16
May 1	.48	.54	-.22	.44	.52	-.10	-.26	-.31	.01	.36	.24
June 1	.36	.27	.15	.35	.15	.14	-.31	-.46	-.18	.54	.03
July 1	.02	.14	-.24	.20	.29	-.70*	-.38	-.32	-.21	.44	.11
Average maximum air temperature											
May	-.42	-.24	-.26	-.22	-.19	.02	-.19	-.32	-.38	.01	-.49
June	-.58	-.72*	.35	-.63*	-.70*	.24	.48	.70*	.29	-.75*	-.30
July	-.34	-.03	-.54	.07	.01	-.43	-.64*	-.59	-.64*	-.06	-.29
Average maximum soil temperature at 5 cm											
May	-.37	-.14	-.36	-.38	.06	-.12	.06	-.04	.04	.15	-.49
June	-.34	-.42	.18	-.37	.34	-.02	-.34	.55	.19	-.51	-.14
July	-.13	.17	-.56	.24	.28	-.77**	-.77**	-.68*	-.58	.36	-.15
Average wind velocity											
May	.29	.53	-.54	.50	.69*	-.83**	-.58	-.63*	-.35	.64*	.32
June	-.10	-.18	.18	-.26	-.01	-.25	.22	.31	.43	.28	-.05
July	-.22	-.16	-.10	.10	-.20	-.04	-.09	-.05	-.48	-.30	-.11

[1]Measured as electrical resistance, thus a negative coefficient means a positive relationship with soil moisture.

Table 3.—*Correlation coefficients (r) between selected weather factors and dry herbage production by vegetation classes and by major species on a deep soil, northeast exposure, 7,100 ft (2 164 m) elevation site (probability: * = >95%; ** = >99%)*

Weather factors	Total vegetation	Total graminoids	Total forbs	*Agropyron spicatum*	*Festuca idahoensis*	*Danthonia intermedia*	*Stipa occidentalis*	*Erigeron subtrinervis*	*Geranium viscosissimum*	*Geum triflorum*	*Lupinis serecius*
Precipitation											
Prior Sept. + Oct.	0.18	0.35	0.05	-0.89**	0.31	0.70*	-0.03	0.35	0.34	0.07	0.01
May	.53	.51	.40	.28	.48	.12	.83**	.14	-.05	.33	.19
June	.03	-.42	.26	.27	-.05	-.53	-.19	.02	.02	.51	.07
July	.36	.20	.35	-.01	.08	.17	.28	.35	.34	.24	.50
May + June	.35	-.09	.49	.43	.24	-.43	.31	.09	-.01	.68*	.18
May + June + July	.46	.02	.57	.35	.23	-.27	.39	.24	.16	.68*	.39
Prior Sept.-Oct., + May-July	.62	.27	.64*	-.26	.47	.21	.39	.51	.41	.77**	.42
Soil moisture at 100 cm[1]											
At beginning of growth	.05	.44	.30	.34	-.33	-.43	-.40	.21	.45	.19	.52
May 1	.10	-.42	.35	.18	-.43	-.41	-.01	.25	.57	.27	.13
June 1	-.53	-.65*	-.33	.73*	-.54	-.83**	-.35	-.61	-.40	-.14	-.38
July 1	-.47	-.29	-.44	.57	-.51	-.39	-.19	-.43	-.25	-.62	-.26
Average maximum air temperature											
May	-.12	-.18	-.05	-.52	.10	.10	-.30	-.13	.10	-.01	-.04
June	.35	.73*	.06	-.70*	.57	.86**	.32	.32	.06	.02	.02
July	-.28	.47	-.10	-.15	-.38	-.29	-.01	-.04	.24	-.28	-.26
Average maximum soil temperature at 5 cm											
May	-.07	-.51	.17	-.16	-.01	-.38	-.44	-.03	-.07	.23	.11
June	-.12	-.10	-.10	-.48	.02	.14	-.24	.11	-.07	-.35	.03
July	-.34	-.55	-.14	-.19	-.44	-.30	-.30	.01	.17	-.48	-.05
Average wind velocity											
May	-.33	-.26	-.28	.64*	-.30	-.41	-.33	-.46	-.20	-.39	-.03
June	-.30	-.02	-.37	-.02	-.46	.12	-.04	.02	.02	-.47	-.31
July	-.64*	-.59	-.49	.22	-.40	-.58	-.56	-.56	-.62	-.39	-.59

[1]Measured as electrical resistance, thus a negative coefficient means a positive relationship with soil moisture.

demonstrated by McKendrick and Sharp (1970) who found that the weight of etiolated tillers per *Agropyron cristatum* plant (a direct index to reserves available for growth) was highly correlated ($r = 0.97^{**}$) with subsequent herbage yield. White (1973) concluded that low carbohydrate reserves reduce the initial growth rate which in turn can affect subsequent exponential growth. Besides the direct effect of slowing initial and subsequent growth rates, low carbohydrate stores are likely to place plants at a competitive disadvantage. I found that reducing the vigor of *Agropyron spicatum* and *Festuca idahoensis* by heavy clipping, but not that of competing vegetation, resulted in a 41- to 43-percent decrease in herbage production the following growing season (Mueggler 1970, 1972b).

Thus it appears that reducing carbohydrate reserves of certain mountain grassland plants, whether by grazing, clipping, or fall regrowth, lowers the capacity of these plants to produce well the following year. This may be caused by a lack of start-up carbohydrates as well as reduced ability to compete with associates that have remained vigorous. In either case, fall regrowth probably accounts for lower production the following year and consequently in the negative correlation with fall precipitation.

On range sites where fall regrowth apparently does not adversely affect growth the following year, the climate may permit replacement of carbohydrate reserves after initial regrowth depletion and before winter quiescence. On my mountainous sites, however, air and soil temperatures may have been inadequate for the extended period of growth required for replacement of the carbohydrates depleted by the initiation of fall regrowth. This possibility is supported by the failure of *Festuca idahoensis* production on the northeast exposure to be negatively correlated with fall precipitation. The orientation of the northeast exposure resulted in lower fall temperatures than on the southwest exposure (Mueggler 1971); these lower temperatures may have been inadequate to support fall regrowth of *Festuca idahoensis*. On the other hand, the average date that *Festuca idahoensis* dried on the northeast exposure was October 7, which was 16 days later than on the southwest exposure. Late September and early October precipitation may simply have prolonged *Festuca idahoensis* growth on the northeast exposure while it initiated regrowth on the southwest site. Unfortunately, I did not obtain data on fall regrowth over the 10-year study period to verify a relationship between fall precipitation and fall regrowth.

Stepwise multiple regression analyses were used to help identify the combination of weather variables that would best account for the yearly variation in production of vegetation classes and of several important individual species. Three weather variables were sufficient to account for at least 88 percent of the yearly variation in production of all classes and species evaluated on the southwest exposure (table 4). Ninety-seven percent of the variation in the production of total graminoids on the southwest exposure was accounted for by a model incorporating prior September-October precipitation, July precipitation, and July wind. The three-parameter models were less effective in accounting for production variability on the more productive northeast exposure (table 5). Although 97 percent of the variation in *Agropyron spicatum* was accounted for by a model comprised of prior September-October precipitation, July 1 soil moisture, and June soil temperature, models for the other species and vegetation classes accounted for only 54 to 82 percent of the variation.

Different combinations of weather parameters best accounted for production variations of different classes and species. This supports the previous conclusion that species differ in their response to the same environmental factors. Contrary to expectations, however, the best-fit models for like vegetation classes and like species differed appreciably between the southwest and northeast exposure. Only in the case of *Agropyron spicatum* did models selected for one site perform well on the opposing site. The best model for this species on the southwest exposure had a coefficient of multiple determination (R^2) of 0.92^{**} on the southwest exposure and 0.94^{**} on the northeast exposure; the best model on the northeast exposure had an R^2 of 0.97^{**} on the northeast exposure and 0.90^{**} on the southwest exposure. In no other instance did the model best fitting one site exceed an R^2 of 0.55 on the opposing site. Yet, both sites were occupied by the same general type of vegetation, were at the same elevation and within 600 ft (183 m) of one another, but on opposite exposures. This suggests that great care should be exercised in extending to broad areas models developed at a single location, especially on environmentally variable mountainous rangelands.

Table 4a.—*Multiple linear regression of best three weather variables selected for predicting dry herbage production by vegetation classes and four major species on a shallow soil, southerly exposure at 2 164 m elevation*

	Total vegetation	Total graminoids	Total forbs	*Agropyron spicatum*	*Festica idahoensis*	*Galium boreale*	*Pedicularis contorta*
Regression constant (kg/ha)	1 577	954	1 214	455	2 310	294	208
	Coefficients						
Weather variables:							
Precipitation (inches):							
Prior Sept.-Oct.	-122	-109		-36			-15
July		- 29				4.2	
Soil moisture at 100 cm depth (log ohms resistance):							
At beginning of growth	-140		-127				-18
On June 1	71		77				
On July 1					-838		
Temperature (°F):							
Air, average max. May			-8.5		-8.0		
Air, average max. June						-5.7	
Soil, 5 cm, average max. June				-7.1			
Wind (average mi/h)							
May					195		
June						18	
July		-47		15			-5.8
Coefficient of multiple determination (R^2)	0.88**[1]	0.97**	0.93**	0.92**	0.94**	0.96**	0.88**
Standard error of estimate (kg/ha)	39.0	22.9	16.9	13.2	20.7	3.1	4.2
Average production (kg/ha)	766	407	359	65	248	49	48

[1]Probability: * = >95%; ** = >99%.

Table 4b.—*Multiple linear regression of best three weather variables selected for predicting dry herbage production by vegetation classes and four major species on a shallow soil, southerly exposure at 7,100 ft elevation*

	Total vegetation	Total graminoids	Total forbs	*Agropyron spicatum*	*Festuca idahoensis*	*Galium boreale*	*Pedicularis contorta*
Regression constant (lb/acre)	1,407	851	1,083	406	2,061	262	186
	Coefficients						
Weather variables:							
Precipitation (inches):							
Prior Sept.-Oct.	-109	-97		-32			-13
July		-26				3.7	
Soil moisture at 100 cm depth (log ohms resistance):							
At beginning of growth	-125		-113				-16
On June 1	63		69				
On July 1					-748		
Temperature (°F):							
Air, average max. May			-7.6		-7.1		
Air, average max. June						-5.1	
Soil, 5 cm, average max. June				-6.3			
Wind (average mi/h)							
May					174		
June						16	
July		-42		13			-5.2
Coefficient of multiple determination (R^2)	0.88**[1]	0.97**	0.93**	0.92**	0.94**	0.96**	0.88**
Standard error of estimate (lbs/acre)	34.8	20.4	15.1	11.8	18.5	2.7	3.7
Average production (lb/acre)	684	363	320	58	221	44	43

[1]Probability: * = >95%; ** = >99%.

Table 5a.—*Multiple linear regression of best three weather variables selected for predicting dry herbage production by vegetation classes and four major species on a deep soil, northerly exposure at 2 164 m elevation*

Regression constant (kg/ha)	Total vegetation -10 004	Total graminoids -790	Total forbs -7 825	*Agropyron spicatum* 282	*Festuca idahoensis* 587	*Geranium viscosissimum* 150	*Lupinus serecius* 404
	Coefficients						
Weather variables:							
Precipitation (inches):							
Prior Sept.-Oct.				-24			
May							26
June					17		
May-June	174						
Prior Sept.-Oct. and May-July		-6.6	292				
Soil moisture at 100 cm depth (log ohms resistance):							
At beginning of growth	345					29	83
On May 1					-24		
On June 1			-412		-121		-176
On July 1			2,202	39			
Temperature (°F):							
Air, average max. June	154	31					
Soil, 5 cm, average max. June				-5.0			
Soil, 5 cm, average max. July						4.9	
Wind (average mi/h):							
July		-121				-85	
Coefficient of multiple determination (R^2)	0.72*[1]	0.65	0.65	0.97**	0.54	0.77*	0.82*
Standard error of estimate (kg/ha)	176	83	157	6	34	23	28
Average production (kg/ha)	1 471	446	1 025	43	170	114	167

[1]Probability: * = >95%; ** = >99%.

Table 5b.—*Multiple linear regression of best three weather variables selected for predicting dry herbage production by vegetation classes and four major species on a deep soil, northerly exposure at 7,100 ft elevation*

Regression constant (lb/acre)	Total vegetation -8,924	Total graminoids -705	Total forbs -6,980	*Agropyron spicatum* 195	*Festuca idahoensis* 533	*Geranium viscosissimum* 134	*Lupinus serecius* 361
	Coefficients						
Weather variables:							
Precipitation (inches):							
Prior Sept.-Oct.				-20			
May							23
June					15		
May-June	155						
Prior Sept.-Oct. and May-July		-5.9	261				
Soil moisture at 100 cm depth (log ohms resistance):							
At beginning of growth	308					26	74
On May 1					-21		
On June 1			-368		-108		-157
On July 1			1,965	35			
Temperature (°F):							
Air, average max. June	137	28					
Soil, 5 cm, average max. June				-4.5			
Soil, 5 cm, average max. July						4.4	
Wind (average mi/h):							
July		-108				-76	
Coefficient of multiple determination (R^2)	0.72*[1]	0.65	0.65	0.97**	0.54	0.77*	0.82*
Standard error of estimate (lb/acre)	157	74	140	6	31	21	25
Average production (lb/acre)	1,312	398	914	38	152	102	149

[1]Probability: * = >95%; ** = >99%.

Variation in Seasonal Development

Apparent growth activity in the spring on these mountain grasslands frequently began at different times for the various species and usually spanned an almost 3-week period (tables 6, 7, and 8). *Lomatium cous, Zigadenus venenosus, Fritillaria pudica*, and *Anemone patens* were among the earliest to begin growth and *Lupinus serecius, Gaillardia aristata*, and *Antennaria rosea* were among the last. Growth usually began almost 1 week later on the northeast than on the southwest exposure. This lag also varied with species, averaging as many as 11 days later for *Oxytropis serecia* and as few as 3 days for *Cerastium arvense*. The lag in growth on the northeast exposure was probably caused by an average 9-day later melt of the winter snowpack on the northeast than on the southwest exposure. Growth of the earliest species usually began within 1 week following snowmelt. During the first 5 years of this study I found that an 1,100 ft (335-m) elevational increase delayed the beginning of growth for individual species from 19 to 37 days, or an average of 28 days for all species (Mueggler 1972a).

The greatest difference between years in which growth began was 43 days for *Linum perenne*; the least difference was 20 days for *Agoseris glauca* and *Achillea millifolium* on the southwest exposure. With most species, however, the difference between the earliest and latest starting dates for growth over the 10-year period was from 25 to 30 days. Most of the species should begin growth in 2 out of 3 years within 8 to 12 days of their mean date for beginning growth. Costello and Price (1939) recorded up to 50 days variation in the beginning of growth for some species over a 10-year period on mountain herblands in Utah. I found no significant difference between exposures in the amount of this year-to-year variation.

The onset of flowering of the various forbs generally spread over almost a 10-week period. The early spring flowers such as *Lomatium cous, Anemone patens*, and *Fritillaria pudica* usually bloomed within 1 to 2 weeks following the start of growth. The floral display then progressed through the growing season until the late-flowering species such as *Erigeron subtrinervis, Gaillardia aristata, Campanula rotundifolia*, and *Galium boreale* began blooming over 2 months later. The flowering sequence of the various species is the order of species names listed in tables 6, 7, and 8. The different grasses usually bloomed within a 2-week period, 8 to 10 weeks after growth began and 2 to 4 weeks after their flower stalks appeared. The various species of forbs and grasses bloomed from 1 to 10 days later on the northeast exposure than on the southwest exposure; this delay averaged 6 days for all species, about the same as the delay in start of growth. Generally the delay was longer and coincided more with the delay in start of growth for the early-blooming species than for those that bloomed later. Apparently, the effects of exposure on flowering tend to become ameliorated as the season advances. Costello and Price (1939) observed that development on north exposures lagged about 10 days behind that on south exposures on mountain herblands in Utah, whereas Bliss (1956) found only a 2- to 4-day lag on north exposures in the alpine tundra of southern Wyoming. An 1,100-ft (335-m) elevational rise caused blooming of individual species on these mountain grasslands to be delayed from 11 to 29 days, or an average delay of 20 days for all species (Mueggler 1972a).

Maximum year-to-year differences in initiation of flowering ranged from 5 to 52 days, and averaged 23 days for all species. There could therefore be as many as 23 days difference between early and late years in the floral display. The flowering date of late-blooming species varied considerably less between years than did that of early-blooming plants. In 2 out of 3 years, the late-blooming species can be expected to flower within 4 to 6 days of their respective average flowering date, whereas the early-blooming species can be expected to flower within about 10 days of their average date. The amount of yearly variability did not differ significantly between exposures.

The duration of flowering (from first bloom to when blooming ceased) was conspicuously species-dependent. Some forbs such as *Agoseris glauca, Zigadenus venenosus*, and *Antennaria rosea* completed their flowering phase on the average within 2 weeks. Others, such as *Lomatium cous, Frasera speciosa*, and *Achillea millefolium* took as long as 4 weeks to finish blooming. The length of the flowering period did not appear related to whether a species tended to bloom early or late in the growing season, nor was it significantly related to exposure.

The start of seed dissemination in the forbs stretched over an 8-week period, usually beginning in early July with *Agoseris glauca* and *Anemone patens*, and ending in late August with *Achillea millefolium, Erigeron subtrinervis*, and *Gaillardia aristata*. The composites were usually among the last to begin dissemination, averaging about 2 weeks later than the average of the other forbs. From 1 to 2 months usually elapsed between initiation of flowering and initiation of seed dissemination. Some species, such as *Agoseris glauca, Cerastium arvense*, and *Polygonum bistortoides* began seed dissemination within about 4 weeks following the onset of flowering, whereas others such as *Fritillaria pudica* and *Lomatium cous* required almost 9 weeks. The grasses usually required about 3 to 4 weeks to form ripe seed from the time they began to flower. Although a considerable lag in seed dissemination occurred on the northeast exposure for some species, such as an average 11 days for *Dodecatheon conjugans*, the mean dissemination date for all species did not differ significantly between exposures because of the high variability among species.

Maximum variation between years in the start of dissemination ranged from less than 3 weeks for *Zigadenus venenosus, Geum triflorum*, and *Polygonum bistortoides* to over 6 weeks for *Pedicularis contorta* and *Agoseris glauca* on the southwest exposure. The average variation between years for all forbs amounted to 26 days. This was similar to the average yearly variation in flowering. Overall, dissemination can be expected to start in 2 out of 3 years within 8 days of the average

Table 6.—*Range, mean, and standard deviation (s) of phenological event dates for prominent forbs on a mountain grassland with a southwest exposure at 7,100 ft (2 164 m) elevation over a 10-year period*

Species	Growth starts			First bloom			Blooming over			Dissemination starts			Plant dried		
	Range	Mean	s	Range	Mean	s	Range	Mean	s	Range	Mean	s	Range	Mean	s
			Days			*Days*			*Days*			*Days*			*Days*
Lomatium cous	4/17-5/12	4/29	10.7	4/20-5/24	5/9	12.0	5/22-6/27	6/12	11.0	6/25-7/23	7/11	8.1	7/10-8/17	7/18	11.8
Anemone patens	4/18-5/16	5/2	9.7	4/26-5/25	5/9	10.3	5/8-6/10	5/25	11.2	6/21-7/16	7/4	8.3	8/15-9/4	8/25	5.8
Fritillaria pudica	4/20-5/16	5/2	9.5	5/2-5/30	5/14	9.4	5/18-6/10	5/31	7.9	7/12-8/5	7/22	6.7	6/25-8/5	7/22	12.0
Dodecatheon conjugens	4/25-5/16	5/5	8.0	5/5-6/3	5/18	10.9	5/15-6/16	6/3	11.6	6/21-7/16	7/5	8.0	6/11-8/1	7/4	14.1
Saxifraga montanensis	4/18-5/14	5/1	9.5	5/8-6/7	5/24	10.1	5/25-6/26	6/12	10.7	6/27-7/16	7/6	6.4	7/10-7/26	7/17	5.2
Agoseris glauca	4/26-5/16	5/5	8.3	5/16-7/7	6/2	14.7	5/25-7/17	6/12	14.2	6/15-9/4	7/1	23.9	7/1-8/16	7/17	13.8
Frasera speciosa	4/23-5/20	5/5	10.0	5/10-6/18	6/4	11.5	6/19-7/11	7/3	7.1	7/6-8/1	7/22	7.8	7/15-9/2	8/13	15.9
Geum triflorum	4/23-5/18	5/4	8.6	5/17-6/12	6/4	9.2	5/30-6/30	6/19	10.3	7/9-7/26	7/17	6.3	8/15-9/19	8/29	12.2
Delphinium bicolor	4/21-5/20	5/6	10.9	5/22-6/26	6/9	12.2	6/8-7/18	7/1	12.1	6/25-7/23	7/11	9.5	6/20-8/14	7/15	15.1
Polygonum bistortoides	4/23-5/16	5/4	8.0	6/1-6/23	6/12	7.0	6/29-7/20	7/7	6.2	7/2-7/20	7/12	5.7	7/17-8/2	7/25	5.1
Cerastium arvense	4/25-5/20	5/7	8.7	5/28-6/27	6/13	9.8	6/18-7/12	7/1	7.7	7/2-7/26	7/12	7.9	7/30-9/5	8/12	11.0
Oxytropis serecia	4/18-5/16	5/2	10.1	6/6-7/3	6/20	9.0	7/2-7/19	7/9	5.1	7/16-8/18	8/4	8.5	8/11-9/30	9/6	20.3
Commandra umbellata	4/28-5/25	5/10	9.6	6/4-6/28	6/21	7.0	6/28-7/18	7/9	6.4	—	—	—	9/6-10/10	9/22	10.4
Zygadenus venenosus	4/18-5/14	5/1	9.8	6/6-7/5	6/23	8.4	6/25-7/16	7/9	6.1	8/2-8/12	8/8	5.6	6/26-8/16	7/27	15.4
Pedicularis contorta	4/25-5/21	5/9	9.3	6/1-7/14	6/24	14.8	6/15-7/27	7/11	14.5	6/25-8/11	7/26	15.4	7/22-9/2	8/15	17.9
Lupinus serecius	5/10-6/2	5/21	7.3	6/18-7/5	6/28	6.5	7/12-7/30	7/23	7.2	8/1-8/18	8/6	5.9	8/12-9/8	8/29	10.4
Antennaria rosea	5/3-5/30	5/16	9.7	6/12-7/6	6/29	7.9	7/1-7/20	7/12	5.5	7/14-8/10	7/27	7.6	—	—	—
Achillea millefolium	4/28-5/18	5/6	7.5	6/23-7/15	7/6	8.1	7/21-8/10	8/1	7.0	8/11-9/6	8/30	7.6	8/16-9/27	9/2	11.8
Linum perenne	4/20-5/22	5/6	10.7	6/30-7/12	7/6	4.5	7/16-8/5	7/25	6.8	7/22-8/19	8/10	9.0	8/26-10/2	9/16	12.4
Galium boreale	5/7-5/24	5/15	7.2	7/8-7/18	7/11	3.3	7/28-8/14	7/31	5.5	8/6-9/8	8/20	9.3	8/23-9/18	9/5	9.2
Gaillardia aristata	5/3-5/28	5/17	8.9	7/11-7/22	7/15	3.8	7/18-8/12	8/1	6.4	8/11-9/3	8/23	7.2	8/20-9/24	9/6	11.9
Campanula rotundifolia	4/24-6/6	5/8	13.3	7/12-7/24	7/17	4.1	7/26-8/13	8/4	6.2	8/6-8/28	8/17	6.6	8/14-9/28	9/4	14.1

Table 7.—*Range, mean, and standard deviation (s) of phenological event dates for prominent forbs on a mountain grassland with a northeast exposure at 7,100 ft (2 164 m) elevation over a 10-year period*

Species	Growth starts			First bloom			Blooming over			Dissemination starts			Plant dried		
	Range	Mean	s	Range	Mean	s	Range	Mean	s	Range	Mean	s	Range	Mean	s
			Days			*Days*			*Days*			*Days*			*Days*
Lomatium cous	4/23–5/20	5/7	10.0	5/2–6/3	5/18	11.7	6/1–7/5	6/19	10.4	6/28–7/26	7/14	7.0	7/12–7/30	7/19	5.9
Anemone patens	4/27–5/22	5/9	9.6	4/30–6/2	5/18	10.3	5/15–6/13	6/3	9.6	6/20–7/20	7/7	8.4	8/18–9/19	8/30	8.7
Fritillaria pudica	4/23–5/20	5/8	10.0	5/6–5/29	5/19	8.0	5/22–6/16	6/7	9.2	7/13–8/1	7/23	6.4	7/10–8/3	7/24	7.1
Dodecatheon conjugens	4/24–5/22	5/9	10.4	5/8–6/4	5/26	8.4	5/30–6/30	6/16	9.6	7/9–7/24	7/16	4.8	7/15–7/28	7/19	5.3
Saxifraga montanensis	4/24–5/22	5/8	11.6	5/15–6/8	6/2	7.8	6/5–7/1	6/19	9.3	6/20–7/27	7/9	10.0	7/10–8/5	7/23	9.0
Agoseris glauca	4/27–5/22	5/10	10.7	5/15–6/13	6/3	8.3	6/5–6/25	6/14	10.0	6/9–7/10	7/1	9.2	6/22–9/25	7/20	25.4
Viola adunca	4/28–5/28	5/14	10.8	5/22–6/22	6/8	10.5	6/5–7/9	6/26	10.4	7/12–8/2	7/24	8.1	8/4–9/22	9/11	14.3
Myositis sylvatica	4/27–5/23	5/11	9.9	5/23–6/20	6/10	10.2	6/14–7/14	7/5	8.8	7/5–7/18	7/12	4.8	7/6–8/10	7/23	10.5
Geum triflorum	4/25–5/20	5/8	10.4	5/30–6/19	6/12	7.3	6/12–7/5	6/28	7.3	7/13–8/1	7/23	6.5	8/20–10/7	9/13	16.3
Delphinium bicolor	4/27–5/23	5/10	10.1	5/28–6/27	6/15	9.8	6/12–7/21	7/3	11.7	7/6–7/24	7/14	6.0	7/4–8/5	7/18	8.5
Cerastium arvense	4/28–5/23	5/10	10.3	6/2–6/30	6/19	9.9	6/28–7/15	7/8	6.4	7/9–7/27	7/18	4.5	7/30–9/10	8/20	11.6
Polygonum bistortoides	4/26–5/22	5/9	10.1	6/5–6/30	6/19	7.4	7/1–7/16	7/10	6.6	7/7–7/23	7/15	4.8	7/18–8/7	7/29	5.8
Phlox multiflora	4/28–5/23	5/12	9.3	6/5–7/5	6/20	9.6	6/30–7/19	7/11	7.2	7/18–8/12	8/3	8.3	8/20–10/3	9/15	12.4
Oxytropis serecia	4/26–6/2	5/13	11.2	6/10–7/9	6/27	9.0	6/30–7/24	7/13	8.6	7/31–8/24	8/10	7.1	8/20–9/28	9/17	11.8
Zygadenus venenosus	4/26–5/21	5/9	10.4	6/18–7/11	7/2	5.9	7/9–7/19	7/13	3.8	7/28–8/18	8/11	6.5	7/14–8/18	8/5	10.9
Antennaria rosea	5/6–6/5	5/24	10.6	6/17–7/13	7/3	8.7	6/30–7/26	7/17	7.7	7/22–8/9	7/31	5.7	—	—	—
Lupinus serecius	5/10–6/7	5/28	8.7	6/24–7/13	7/4	6.5	7/12–8/2	7/22	7.6	7/15–8/12	8/4	8.4	8/13–9/15	8/30	12.0
Achillea millefolium	4/28–5/28	5/13	10.9	6/30–7/13	7/10	5.0	7/29–8/23	8/6	8.2	8/8–9/10	8/27	10.7	7/26–9/20	8/30	16.7
Linum perenne	4/28–5/25	5/13	10.0	7/3–7/16	7/11	4.5	7/16–8/4	7/27	6.7	7/26–8/30	8/16	9.7	9/13–10/10	9/27	7.8
Galium boreale	5/6–6/3	5/19	9.1	7/11–7/22	7/16	3.8	7/22–8/10	8/1	5.1	—	—	—	8/20–9/18	9/7	10.6
Gaillardia aristata	5/10–6/10	5/26	9.6	7/15–7/24	7/18	3.3	7/24–8/12	8/3	5.6	8/14–9/10	8/28	9.2	8/26–9/25	9/9	10.8
Campanula rotundifolia	4/26–5/26	5/12	11.2	7/17–7/22	7/19	1.6	7/31–8/16	8/8	5.2	8/12–9/4	8/22	6.8	8/19–9/14	9/4	8.0
Erigeron subtrinervis	5/4–6/1	5/18	9.4	7/20–7/27	7/23	2.9	7/30–8/26	8/14	8.8	8/15–9/6	8/29	7.4	9/4–10/5	9/21	9.2

Table 8.—*Range, mean, and standard deviation (s) of phenological event dates for prominent grasses on southwest and northeast exposures at 7,100 ft (2 164 m) elevation over a 10-year period*

Species	Growth starts			First bloom			Blooming over			Dissemination starts			Plant dried		
	Range	Mean	s	Range	Mean	s	Range	Mean	s	Range	Mean	s	Range	Mean	s
			Days			*Days*			*Days*			*Days*			*Days*
SOUTHWEST EXPOSURE															
Danthonia intermedia	4/28–5/24	5/12	10.2	6/10–7/4	6/25	7.8	6/29–7/20	7/9	6.2	7/22–8/10	7/30	6.3	8/18–10/15	9/25	17.4
Festuca idahoensis	4/21–5/16	5/4	10.0	5/22–6/30	6/14	13.2	7/6–7/18	7/13	4.1	7/25–8/17	8/5	6.2	8/27–10/15	9/21	16.8
Stipa occidentalis	4/28–5/28	5/10	10.8	6/1–7/5	6/24	10.6	7/13–7/24	7/18	3.5	7/21–8/15	8/7	8.0	8/30–10/20	9/20	16.6
Agropyron spicatum	4/25–5/18	5/6	8.3	6/1–7/3	6/22	9.5	7/12–7/25	7/19	3.6	8/16–8/23	8/19[1]	3.8	9/6–10/7	9/22	8.9
NORTHEAST EXPOSURE															
Danthonia intermedia	4/28–5/29	5/16	11.9	6/8–7/8	6/27	10.0	7/1–7/21	7/13	7.3	7/26–8/12	8/3	6.1	9/10–11/2	10/6	13.6
Festuca idahoensis	4/25–5/23	5/8	11.1	5/24–6/29	6/17	12.4	7/3–7/24	7/16	6.2	7/28–8/21	8/11	7.2	8/25–11/1	10/7	18.0
Stipa occidentalis	4/29–5/29	5/17	9.5	7/1–7/12	7/7	4.0	7/17–7/27	7/22	3.1	7/26–8/18	8/10	7.4	9/2–10/20	9/25	14.4
Agropyron caninum	5/1–5/30	5/16	11.6	6/10–7/15	6/29	12.2	7/9–7/29	7/22	5.3	8/17–8/28	8/24	3.7	8/27–10/6	9/19	11.8
Agropyron spicatum	5/1–5/28	5/14	9.7	6/12–7/8	6/25	8.3	7/16–7/29	7/23	3.9	—	—[1]	—	9/4–10/5	9/22	10.0
Bromus anomalus	4/28–5/28	5/16	10.8	6/23–7/9	7/1	5.1	7/20–7/29	7/26	2.7	8/18–9/2	8/25	4.5	8/30–10/12	9/22	13.5

[1]Maturing seed usually destroyed by insects.

date. The seed-ripe stage for grasses generally can be expected to occur in 2 out of 3 years within about 6 days of the average date.

Those forbs that tended to bloom early in the season also tended to dry early, with the exception of the apparently deeply rooted *Anemone patens* which tended to dry fairly late. With *Anemone patens* excluded, the average drying date of the early blooming species preceded that of the late bloomers by about 7 weeks. The grasses were generally the last to dry, averaging about 2 weeks later than the late forbs. Growth activities with some forbs virtually ceased once the seed had matured and began dissemination. Other species continued to remain green and photosynthetically active for up to 2 months following the seed-ripe stage. *Dodecatheon conjugens, Fritillaria pudica, Delphinium bicolor*, and *Zigadenus venenosus* typified those species that ceased growth activity with the production of seed. *Geum triflorum, Linum perenne, Viola adunca, Anemone patens*, as well as most grasses, continued with a substantial period of growth following seed production. Although some species tended to dry earlier on the southwest than on the northeast exposure, others did not; the average difference between exposures was not significant because of this variability between species. Earlier I found that the forbs on these grasslands dried an average 18 days later and the grasses 10 days later at sites 1,100 ft (335 m) higher in elevation (Mueggler 1972a).

The between-year variation in the date of drying amounted to as much as 6 to 8 weeks for some species (*Agoseris glauca, Achillea millefolium, Danthonia intermedia, Festuca idahoensis*), and as little as 3 weeks for others (*Saxifraga montanensis* and *Polygonum bistortoides*). Except for those forbs that tended to dry early in the season upon completion of seed production, the drying date appeared to be controlled primarily by the availability of soil moisture adequate for growth. Generally, the forbs and grasses on these mountain grasslands can be expected to dry in 2 out of 3 years within about 12 days of their mean drying date.

Although most species apparently became dormant for the remainder of the year following drying, several produced new leaves again in the fall in some years. This regrowth occurred most regularly with *Geum triflorum, Saxifraga montanensis*, and *Cerastium arvense*, and to a lesser degree with the grasses. Fall regrowth in *Geum triflorum* and *Saxifraga montanensis* was in the form of a small rosette of new leaves within the outer rosette of dried leaves. Regrowth of *Cerastium arvense* was in the form of small leaves in the axils of dried leaves distributed along the stems.

The duration of growth, that span of time between the start of growth and when the plants dried, differed appreciably between species. On these 7,100-ft (2 164-m) elevation sites, the mean duration of growth over the 10-year period varied from 60 to 150 days. The following forbs completed their growth cycle in less than 80 days: *Agoseris glauca, Delphinium bicolor, Dodecatheon conjugens, Fritillaria pudica, Lomatium cous, Myosotis sylvatica*, and *Saxifraga montanensis*. Those forbs that remained active on the average an excess of 115 days were: *Campanula rotundifolia, Comandra umbellata, Erigeron subtrinervis, Geum triflorum, Linum perenne, Oxytropis serecia*, and *Viola adunca*. The grasses generally remained photosynthetically active for a considerably longer period (125 to 150 days) than most of the forbs.

Although duration of growth varied appreciably among both species and years, it did not differ significantly between exposures. Duration of growth was generally about 1 week shorter at 8,200 ft (2 500 m) than at 7,100 ft (2 164 m) elevation (Mueggler 1972a). For species common to both elevations, the growth period averaged 94 days at 8,200 ft (2 500 m) and 103 days at 7,100 ft (2 164 m) over a 5-year period.

Relation of Seasonal Development to Weather

Blaisdell (1958) concluded that high temperatures hasten at least the early phases of plant development. For example, he found a significant negative correlation between March-April mean temperature and the dates of the appearance of flower stalks for eight native perennial species on sagebrush-grass rangelands ($r = -0.62^{*}$), and between March-May mean temperature and the dates of full bloom ($r = -0.93^{**}$). On the other hand, he found that development during the latter part of the growing season apparently was most closely related to precipitation; for example, the dates that plants dried in his study were positively correlated with April-May precipitation ($r=0.82^{**}$). Costello and Price (1939) determined that above normal, evenly distributed rainfall during the summer extended the period required for the ripening of seed on mountain herblands.

Seven weather variables expected to affect development rate were selected to examine the relation between weather and phasic development on mountain grasslands: May heat-sum, May-June heat-sum, heat-sum to first bloom, June precipitation, May-June precipitation, July 1 soil moisture, August 1 soil moisture. Heat-sum (degree-days) was computed by averaging the maximum and minimum air temperatures daily and accumulating the number of degrees this average exceeded 5° C. The 5° C critical level was selected because Larcher (1980) maintains that, as a rule, terrestrial vascular plants are active in the production of dry matter and growth only between 5° C and 40° C.

Weather was not monitored sufficiently in advance of the start of growth to permit determining what factors related to this stage. Obvious growth activity usually began shortly after snowmelt. The start of growth for some plants was uncertain, however, because small green leaves were frequently present at the time of snowmelt. These either began growth under the winter snowpack, or more likely overwintered from fall regrowth. Most conspicuous among these species were *Saxifraga montanensis* and *Geum triflorum*, and occasionally *Festuca idahoensis* and *Agropyron spicatum*. Mooney and Billings (1960) observed that the alpine species *Saxifraga rhomboidea, Geum rossii*, and *Polygonum bistortoides* frequently began growth under the snow.

The day of the year that flower stalks in *Festuca idahoensis* and *Agropyron spicatum* appeared was significantly negatively correlated with both May and May-June heat-sums. These correlation coefficients ranged between −0.63 and −0.75. in other words, the warmer the May and June temperatures, the sooner flower stalks appeared, which supports the findings of Blaisdell (1958).

Flowering date also was closely associated with either May or May-June heat-sums. Of the 16 species tested, 11 were correlated significantly with these temperature measures. Almost all correlation coefficients regardless of statistical significance were negative, suggesting that warmer May and June temperatures speeded up the flowering process. The significant correlation coefficients ranged from −0.64 for the *Myositis sylvatica*/May heat-sum to −0.85 for the *Festuca idahoensis*/May heat-sum. Cumulative degree-days until first bloom lacked consistency between years for any given species. The coefficient of variations for degree-days until first bloom ranged from approximately 15 percent for late blooming species to approximately 75 percent for early bloomers. This suggests either that flowering of these species is not rigidly dependent upon cumulative degree-days, or that the heat-sum measure used was inadequate to detect this dependency.

Seed ripening was significantly correlated with weather in only 5 of the 16 species tested. Most of these relationships were again with May heat-sums. The correlation coefficients were negative as they were with flowering. Since seed ripening of the species involved usually did not occur until at least early July and since flowering of most of these same species was significantly correlated with May heat-sum, the significant correlation between May heat-sum and ripening very likely results from a high correlation between flowering and seed maturation. *Gaillardia aristata* and *Phlox multiflora*, both relatively late maturing, were the only species where seed ripening was significantly correlated with May-June precipitation ($r = 0.68$ and 0.71 respectively). These two species delayed maturation in years with greater than average precipitation in May and June.

CONCLUSIONS AND IMPLICATIONS

While average forage production on native rangelands sets the average stocking rate, yearly variation in production determines annual adjustments in stocking that may be required. This study indicates that total herbage production on mountain grassland ranges can be expected to fall within 85 to 90 percent of the long-term mean in 2 out of 3 years. The yearly variability in production of vegetation classes and of individual species is considerably greater. If stocking depends primarily upon the amount of grasses, forage production can be expected to fall within approximately 75 percent of the long-term mean two-thirds of the time; however, if forbs are the primary forage source, forage production can be expected to be within 80 to 85 percent of the mean in 2 out of 3 years. Production of individual species can be expected to be within only 33 to 76 percent of long-term means in 2 out of 3 years, depending upon the species. A "good" year for production of grasses is neither a good nor a poor year for forb production on these mountain grasslands. Species apparently react differently to subtle differences in weather. Increased yields of one often compensate for decreased yields of another and thus reduce yearly differences in total production. Although northerly exposures are generally more productive than southerly exposures, the relative amount of yearly variation in production is similar.

Although over 88 percent of the year-to-year variation in production of vegetation classes and of abundant species on the study site was accounted for by models incorporating only three weather parameters, applying such models beyond the immediate site can be hazardous. Models developed for one exposure seldom performed well on the opposing exposure for the same vegetation classes and species, even though the vegetation and many environmental characteristics were fairly similar. One cannot, therefore, assume without further testing that a model suitable for predicting production at one location on mountain rangelands will be applicable to other similar locations.

On these short-season, mountain grasslands a negative relationship may exist between fall regrowth of *Agropyron spicatum* and *Festuca idahoensis* and production the following year. Verification of this relationship should improve predictions of the annual production of these important forage species.

Vegetation begins growth sooner and develops more rapidly in some years than in others. Because date of range readiness for grazing depends upon how rapidly the vegetation develops, the extent of such variation is important to those managers responsible for fixing grazing seasons. In 2 out of 3 years, most mountain grassland species in southwestern Montana can be expected to begin growth within 8 to 12 days of their respective average date for the beginning of growth. Growth usually begins about 1 week later on northerly than on southerly exposures. In 2 out of 3 years, those species that flower early in the season can be expected to bloom within 10 days of their mean flowering date, and those that flower late in the season can be expected to be within 4 to 6 days of their mean date. Flowering generally occurs about 1 week later on northerly than on southerly exposures. From 1 to 2 months usually elapses from the time a species first begins to bloom and when seed begins to disseminate. Two-thirds of the time seed dissemination for most forbs occur within 8 days and for the grasses within 6 days of the average date for each species. Some species dry about 2 months later in some years than in others; generally, however, in 2 out of 3 years the vegetation can be expected to dry within 12 days of the long-term mean date for drying.

Range managers generally rely upon vegetation and soil readiness indicators to decide when grazing can safely begin in the spring or early summer. *Delphinium bicolor* in full bloom and the appearance of *Festuca idahoensis* flower stalks are used as indicators of grazing readiness on mountain grasslands in Montana (U.S. Dept. Agric., Forest Service 1969). Applying these indicators suggests that the date of range readiness can differ as much as 5 weeks over a 10-year

period on these mountain grasslands. In 2 out of 3 years, however, the vegetation on these grasslands should be ready to graze within 2 weeks of the average date of readiness.

Early growth stages, such as the appearance of flower stalks and blooming, appear to be associated with May and June temperatures. As might be expected, warm temperatures speed up these early development stages, and consequently speed up the date of range readiness for grazing.

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Yearly differences in plant development and herbage production of prominent species within the *Festuca idahoensis/Agropyron spicatum* habitat type are documented for a 10-year period. Differences between northeast and southwest exposures at an elevation of 7,100 ft (2 164 m) are discussed. Data are expressed as ranges, means, and standard deviations. Correlation coefficients between production and major weather variables are given, and multiple regression models for predicting production from weather variables are presented.

KEYWORDS: production, seasonal development, phenology, weather effects, variability, mountain grasslands, Montana

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